Differential feeding strategies in phyllidiid nudibranchs on coral reefs at Halmahera, northern Moluccas

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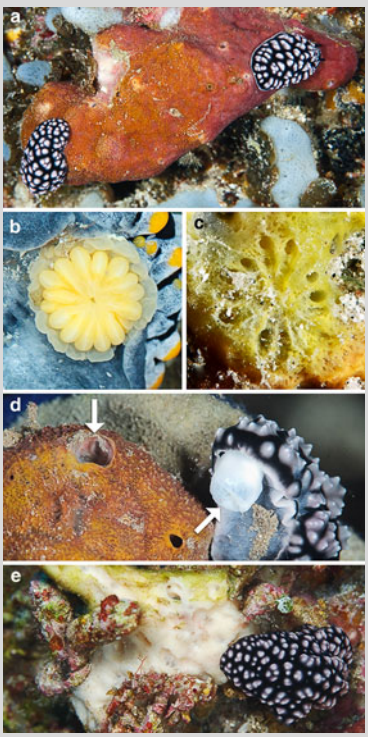

Fig. 1 **a** Individuals of *Phyllidiella nigra* (*left*) and *Phyllidiella pustulosa* (*right*) on the sponge *Axinyssa* aff. *variabilis* **b** Everted pharyngeal bulb of a *Phyllidia varicosa*. **c** Feeding mark in an *Axinyssa* aff. *variabilis* made by a *P. varicosa*. **d** Partly everted pharyngeal bulb of *P. pustulosa* (*right arrow*) that was extracted from a hole in an *Axinyssa* aff. *variabilis* (*left arrow*). **e** *P. nigra* individual feeding on an *Axinyssa* aff. *variabilis*

Sponges frequently produce toxic secondary metabolites, especially in tropical coral reefs. These metabolites are thought to have evolved as a chemically mediated defence mechanism and are highly effective against potential predators (Proksch 1994). Nudibranchs of the family Phyllidiidae feed on sponges of the order Halichondrida and exploit this adaptation: they selectively sequester the toxins and employ them for their own protection (Ritson-Williams and Paul 2007; Cimino and Ghiselin 2009). Other than most dorid nudibranchs, phyllidiids lack radulae and jaws. Rather, they are specialized in suctorial feeding. Their feeding apparatus consists of a small mouth followed by an inflated part of the pharynx known as the pharyngeal bulb, which contains secretory glands and can be everted (Fig. 1b, d), presumably for external digestion (Brunckhorst 1993).

During a biodiversity survey off West Halmahera (northern Moluccas) in 2009, we recorded seven phyllidiid species on six halichondrid species. Sponges were identified by the second author (NJdV). Vouchers are deposited in NCB Naturalis. *Phyllidia varicosa*, *Phyllidiella pustulosa*, and *Phyllidiella nigra* fed almost exclusively on the same sponge host, *Axinyssa* aff. *variabilis* (Fig. 1a), however, using different feeding techniques. *P. varicosa* feeds superficially, consuming little more than its host's skin, often leaving a pattern of multiple discoloured, rosette-shaped marks (Fig. 1c). In contrast, *P. pustulosa* inserts its exceptionally large pharyngeal bulb deep into the host sponge, frequently creating a narrow hole as deep as half its own length (Fig. 1d). Finally, *P. nigra*, which has a pharyngeal bulb similar to that of *P. pustulosa*, yet not quite as large, appears to consume consecutive chunks of tissue from the host's surface; in one instance, little of the exposed surface was left untouched (Fig. 1e). Dissection of two specimens of each species revealed a significant amount of whole spicules belonging to *Axinyssa* aff. *variabilis* in the digestive tracts of *P. nigra* and *P. pustulosa*, but not in *P. varicosa*.

In conclusion, *P. varicosa*, *P. pustulosa*, and *P. nigra* differ in the way they exploit their mutual host, and this difference may facilitate their coexistence in species-rich coral reefs.

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